

COMMUNAL DISAFFECTION IN ANTS

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It has been generally accepted that ants are perfectly loyal to the group to which they belong, despite the regular disloyalty of parasitic queens and despite some rather infrequent exceptions to this rule. Many of these exceptions were collected by the present author in "Punitive Behavior of Ants,"¹ and since the publication of that article the author has observed occasional fighting among the workers of a nest of *Formica neocinerea*. The belief in formicine loyalty has brought about the particular assumption, by the writer no less than by all other myrmecologists, that when ants affiliate with one another, living amicably together for a few days, cleaning one another and interregurgitating; then the union between them is permanent and indissoluble.² Two sets of observations show that this assumption is not always correct, and suggest a possible method of origin of the temporary parasites from more normal ants.

The first case is that of a nest of *Formica subsericea* which I started in the fall of 1934 by collecting several queens after their nuptial flight. By the fall of 1935, when the nest contained three queens and a number of eggs and larvæ, hostility among the queens was first observed. Around September 1, twenty workers were born, and soon thereafter one of the queens was dismembered by another and by several workers. A second queen was attacked, and rescued only after a foreleg was permanently paralyzed.

Somewhat the same thing happened the next time I obtained queens of this species. This was on August 8, 1940. On Sep-

¹ The Journal of Comparative Psychology, June, 1940, p. 327.

² An exception must be noted in the case of Miss Fielde's work, which was recognised by Forel in the last book he wrote. Miss Fielde found that apparently successful affiliation sometimes broke up in a series of fights, so that observation over a period of weeks rather than days was necessary in order to determine the success of affiliation. Even Miss Fielde, however, had no suspicion of the phenomena suggested in this paper.

tember 30, five of the original six queens being still alive, the first worker was born into this nest, which we shall call nest A. The second came on October 1, and on October 2 I noticed two queens attacking a third, one pulling a leg while the other sawed her neck. I separated them, and observed that all the other queens threatened or attacked the victim whenever they met her. On at least one occasion the attack resulted in an exchange of poison. The two workers licked her off at some length, but this did not keep the other queens from attacking her, so that I at length removed her from nest A, placing her, together with the pupa that was nearest maturity, in nest B.

The pupa in nest B hatched on the following day. On October 8 I tried placing the B queen back in nest A but she was again attacked. Neither the two workers that knew her, nor the two born on October 4 joined in the attack. On November 2 the B worker was placed in nest A, and was immediately attacked by the A workers. Queen B lived with the worker until January 16, when the queen died, never having laid an egg.

Now let us return to nest A. The fifth and last pupa hatched on October 10, and at this time one of the four remaining queens, whom we shall call D, began to spend considerable periods away from the others. This continued for two weeks, until I began urging D back to the others, in which efforts one or two of the workers aided me. Eventually I suspected that one of the queens was responsible for D's behavior, so on October 29 I forced D back to the main nest, discovered the particular queen (C) who was attacking her, and removed C to solitary confinement. Two days later, C was allowed to return and was peaceable, while D, who had remained with the others during C's absence, showed resentment for only a few minutes.

C's reform lasted only three days, when she again attacked D, and was placed in solitary for one day. After this she was quiescent for almost two weeks, but then nest A gave increasing evidence of being in a highly nervous state. On November 19 D was again attacked and terrorized; so much so in fact that she was afraid even of the workers, and her fear of the other ants completely obscured her usual timorousness towards me. In addition, D had been unable to approach the water supply until

my removal of C, after which the members of nest A reunited and calmed down within a few hours.

C was replaced in nest A after four days of isolation, during which she laid five eggs. The first workers she met did not behave towards her altogether as towards a nestmate, and she regurgitated to them. All the ants palpated her, and no doubt recognized her as a temporary stranger, but there was no hostility. On the following morning I found C with the larvæ and eggs in the usual compartment, one queen in the food chamber, and D and the remaining queen in still another room; while the nest as a whole was extremely nervous. In the afternoon the three queens, A, D, and E, were together with one worker. I urged them towards the main nest in the water compartment, and they were very reluctant. When I succeeded, moreover, C attacked them until she was removed, whereupon nest A quieted immediately.

C, meanwhile, was allowed to found her own nest, but made little progress because of a tendency to eat her own eggs. On the death of B on January 16, B's worker was caused to affiliate with C, and the nest has made reasonable progress since then.

But let us turn back once more to the three queens remaining in nest A. The nest became so calm with C gone that I could remove the glass cover with less disturbance than was formerly produced by my walking in the same room with them. Fifteen young pupated from December 8 to December 21, but their times of birth unfortunately fell within a period when I was absent, and the record is thus for a time at second hand. Two were born on December 27, two on December 30, one on the 31st, two on January first, and one January 2nd. On January 2nd A and D were fighting, A being supported by one of the older workers. When finally separated, A had lost the right front leg and had the right rear leg paralyzed: D had lost the right antenna, right rear leg, left front leg, and left middle leg. I returned at this juncture, and on the following day found A and E fighting and completed the separation of the nests. The excitement had an unfavorable effect on the workers still unborn, as they were not freed from their membranes at birth and only two of the seven survived.

Something should be said, perhaps, of the subsequent history of A, D, and E. A was prolific and has been progressing rapidly. E was much less so, and ate some of her eggs, so that her progress has been very slow. D had much difficulty in standing or moving, but gradually learned ways of aiding herself. At first she used her mandibles as an extra leg; later she learned to bend her fore-leg under her body in such a way as to get a tripod effect out of her three legs. When she falls over, her only method of righting herself is to push herself on her back to a wall, then to bend over with the posterior of the thorax supported by the wall. Subsequently she took to resting on her back for long periods, which in other ants would imply death. Her crippled condition has not impaired her fertility.

What interpretation is to be placed on the behavior described in this article? We must recognize, to start with, that it is not exceptional but a more or less standard form of behavior with this and probably with related species. It might be supposed that the queens driven out were those whose presence was harmful to the group, either because they were infertile or because they ate the young. This supposition was at first supported by the fact that B, the first queen driven out, proved sterile; but broke down later, since the other queens were all fertile and since C and E, the two outstanding transgressors in the matter of consuming their young, were far from being the principal victims of attack.

The clue to the situation seems to reside in the fact that the outbreak in each case coincided very closely with the maturation of workers. In the first nest, the first batch of twenty workers to mature were born around September 1, and hostilities among the queens occurred only a few days thereafter, although these queens had lived peaceably together for over a year. In the second case, the first batch of six workers were born between September 30 and October 4, and B was attacked and removed on October 2. One worker was born on October 10, and should perhaps be considered one of the first batch: at all events the intransigence of C dates from October 10. This intransigence lasted to November 3; and was renewed and extended on November 19th until her removal on November 24. The renewal of

hostilities was not itself marked by any births, and is probably to be considered merely the continuation of the fighting of October 10. Nevertheless, this period was marked by the most intensive egg-laying in the history of the group. The last batch of workers to mature were ten that were born from December 27 to January 4, plus some five others that died from insufficient attention during this period. Fighting between A and D broke out on January 2, and between A and E on January 3.

As a hypothesis to account for the behavior in question, I suggest an emotion of jealousy between queens, the biological basis of which would be identical with that of jealousy among mammals except that it has reference to the loyalty of the brood rather than to the faithfulness of a mate. Miss Fielde has demonstrated that workers remain friendly with any individuals they are acquainted with in their first few days of life, so that this period is the critical time for associated queens. If any one is driven away for these few days, she will find her return made difficult by the hostility of the new workers, and the advantages of the combined brood will accrue to the remaining queens. At the beginning of their association, the jealousy would be at a minimum and formicine gregariousness in the ascendant, thus permitting affiliation. Affiliation would have the advantage to the associated queens that some of them could forage while others guarded the young. And doubtless cases do occur where the affiliation is permanent.

This hypothesis is not asserted to apply to all ants. *Acanthomyops* queens, for example, refuse to affiliate, and if several are put in a common enclosure, will fight until one only remains alive. *Prenolepsis* queens, on the other hand, are more sociable than the *Formica*. If this behavior, however, is assumed to have been typical in groups wherein the practice of slavery arose, the origin of this instinct becomes a simple matter to explain. If the queen of one strain of an ancestral *Formica* developed increased fighting ability at the expense of its maternal capacities, and intensified its early gregariousness and later jealousy, it would have immediate increased survival value and could readily develop into the temporary parasitism of *rufa exsecta* types, and the permanent parasitism of *sanguinea* and *Polyergus*. A similar development

in other genera may account for the occurrence of temporary parasitism in *Aphanogaster* and other genera and for the Myrmecine degenerates. A further point of some interest is that in two cases described in this paper workers of *Formica subsericea* took sides in the fighting between queens. This indicates that Miss Fielde's principles of affiliation are not altogether adequate; and suggests as well that there may be some correlation with such instances among parasitic ants as the assassination of their own mother by *Monomorium* workers in the presence of *Wheeleriella* parasites.

The existence and prevalence of the suggested jealousy among queens for the favor of workers is supported by two other facts. The first is that, in a long course of observations of many species of ants, it has become evident to the author that affiliation between queens and workers is easier to achieve than affiliation between alien groups of either caste alone. The second point is that in the closely related and socially parallel case of the bees, the jealousy between queens is so strong that it is the predominant factor in the conduct even of related queens in the same hive. It is not at all unlikely that the instinct of jealousy may have its root in the nature of a common ancestor, as well as in the requirements of adaptation to a somewhat similar social structure.